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Invasive ants of Bermuda revisited

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Abstract

For 60+ years, two of the world's most widespread and destructive invasive ant species, the African big-headed ant (*Pheidole megacephala*) from tropical Africa and the Argentine ant (*Linepithema humile*) from subtropical South America, have been engaged in an epic battle on the islands of Bermuda. Both species are completely intolerant of the other and are also well-known for killing off native invertebrates, particularly other ants. Here I surveyed sites across Bermuda in 2016, including resurveys of the locations previously surveyed in 1963, 1966, 1973, 1986, and 2002, to provide an update on this conflict. The status of all other ant species present in the islands, including previous records from literature, is also provided. In addition, I surveyed ants nesting in red mangrove (*Rhizophora mangle*) trees to evaluate whether this arboreal habitat may serve as a refuge for previously overlooked ant species.

In 2016, *L. humile* occurred at most surveyed sites in Bermuda, including all ten resurveyed sites. *Pheidole megacephala* was present at only two resurveyed sites, a lower proportion of sites than any of the five earlier surveys. Still, *P. megacephala* occupied substantial areas, particularly in and around Hamilton, the capital of Bermuda. This survey increased the number of ant species with verified records from Bermuda to 25, including four exotic species recorded for the first time: *Cardiocondyla minutior, Pheidole navigans*, *Strumigenys emmae*, and *Strumigenys membranifera.* I found five ant species nesting in mangroves: *L. humile* plus four Old World exotics, *C. minutior*, *Cardiocondyla obscurior*, *Monomorium floricola*, and *Plagiolepis alluaudi*.

It appears that *L. humile* may be better suited to the subtropical climate of Bermuda than *P. megacephala*, except perhaps in warmer and sunnier habitats, such as plantings along urban streets and in open parks, where *P. megacephala* may hold the advantage. The dataset on the new ant records from 2016 is provided with the paper.

Keywords

Atlantic islands, biodiversity, exotic ants, *Pheidole megacephala*, *Linepithema humile*, tramp ants

Introduction

For more than 60 years, two of the world's most widespread and destructive invasive ant species, the African big-headed ant (*Pheidole megacephala*) from tropical Africa and the Argentine ant (*Linepithema humile*) from subtropical South America, have been engaged in an epic battle on the Atlantic islands of Bermuda. *Pheidole megacephala* was first recorded in Bermuda in 1889 (Dahl 1892), and was the dominant ant species there in the early 20th century (Haskins 1939, Wetterer and Wetterer 2004). When *L. humile* arrived in Bermuda in the 1940s, however, this new invader quickly took over much territory, displacing *P. megacephala*. Still, *P. megacephala* maintained many strongholds, and ever since, these two species have been contesting ever-shifting battlefronts between mutually exclusive territories that together occupy most of the land area of Bermuda (Haskins 1939; Haskins and Haskins 1965, 1988; Crowell 1968; Lieberburg et al. 1975; Wetterer and Wetterer 2004).

Both *P. megacephala* and *L. humile* are well-known for killing off native invertebrates, particularly ants (Erickson 1971; Human and Gordon 1996; Holway 1999; Wetterer et al. 2000, 2001; Wetterer 2002). During their tenure in Bermuda, *P. megacephala* and *L. humile* have almost certainly had a devastating impact on native invertebrates. In addition to the two dominant ant species, Wetterer and Wetterer (2004) reported confirmed records of 18 other ant species from Bermuda. Subsequently, I found museum specimens of two more ant species from Bermuda: *Nylanderia* cf. *fulva* (reported as *Paratrechina pubens*; Wetterer 2007) and *Monomorium floricola* (see Wetterer 2010), bringing the total number of known species to 21 (plus one male specimen identified only to genus; see Results). It is unclear whether any ant species now living in Bermuda are native, i.e., predating human arrival.

In the present study, I surveyed sites across Bermuda to provide an update on this conflict and on the status of other ant species present. In addition, I surveyed ants nesting in red mangrove (*Rhizophora mangle*) to evaluate whether this arboreal habitat may serve as a refuge for some previously overlooked ant species. Red mangroves grow in and adjacent to shallow brackish water in subtropical and tropical estuaries around the world, providing a unique habitat, often completely isolated from any terrestrial habitat.

Methods

In 3–10 May 2016, I surveyed ants in Bermuda. I hand-collected ants using an aspirator, sifted litter using a Davis sifter, and collected ants from inside dead twigs and branches of red mangrove.

To examine changes in which ant species, *P. megacephala* or *L. humile*, dominated specific areas in Bermuda, Haskins and Haskins (1988) re-surveyed ten sites that had been surveyed earlier. Wetterer and Wetterer (2004) surveyed these same ten sites.

In 2016, I again surveyed ants at these ten sites using hand collecting and litter sifting (geo-coordinates and collection date in parentheses):

1. Great Head Park (32.368, -64.650; 9 May 2016)
2. Mullet Bay Road and Ferry Road intersection (32.375, -64.696; 5 May 2016)
3. Leamington Caves (32.342, -64.708; 4 May 2016)
4. Knapton Hill Road and Harrington Sound Road intersection (32.321, -64.716; 4 May 2016)
5. Knapton Hill Road and Harrington 100s Road intersection (32.315, -64.724; 5 May 2016)
6. Christchurch Lane and Brighton Hill Road intersection (32.306, -64.754; 9 May 2016)
7. Spittal Pond Reserve (32.311, -64.724; 5 May 2016)
8. Newstead Hotel (32.284, -64.787; 9 May 2016)
9. Wreck Road (32.276, -64.881; 8 May 2016)
10. Ireland Island (32.327, -64.835; 8 May 2016)

I collected dead twigs and branches of red mangrove into 3.8-liter zip-lock storage bags (3–10 bags from different mangrove trees, depending on the number of accessible trees) at 14 sites in Bermuda (geo-coordinates, collection date, and # of bags in parentheses):

1 Tom Wood's Bay (32.304, -64.814; 3 May 2016; 10)
2. Hungary Bay (32.291, -64.760; 3 May 2016; 10)
3. Crow Lane Park (32.293, -64.771; 3 May 2016; 10)
4. Mangrove Lake (32.326, -64.711; 4 May 2016; 10)
5. Trott's Pond (32.330, -64.702; 4 May 2016; 10)
6. Walsingham Bay (32.346, -64.709; 4 May 2016; 10)
7. Coot Pond (32.389, -64.678; 5 May 2016; 4)
8. Mullet Bay Rd and Ferry Rd (32.375, -64.696; 5 May 2016; 4)
9. Stokes Point Park (32.371, -64.694; 5 May 2016; 3)
10. Blue Hole (32.351, -64.710; 5 May 2016; 10)
11. Fairyland Creek (32.295, -64.802; 6 May 2016; 10)
12. Mill Creek (32.304, -64.801; 7 May 2016; 10)
13. The Lagoon (32.313, -64.844; 8 May 2016; 10)
14. Pilchard Bay (32.276, -64.880; 8 May 2016; 10)

I also did hand collecting and litter sifting in areas adjacent to each red mangrove sites, as well as at numerous other sites when time and weather permitted. On the last day of collecting (10 May 2016), I surveyed 12 urban sites in and around Hamilton city, the capital of Bermuda. In addition, three people (R. Franco, J. Steele, and C. Stringer) sent me samples of ants they collected in and around their homes in Bermuda in May 2016.

I retained all pinned and alcohol specimens in my personal collection.

Results

In 2016, I collected a total of 19 ant species in Bermuda, including four recorded for the first time: *Cardiocondyla minutior, Pheidole navigans*, *Strumigenys emmae*, and *Strumigenys membranifera* (Table 1, See Suppl. material 1. These records bring the total number of confirmed ant species records from Bermuda to 25. Bermuda Department of Agriculture has previously intercepted *P. navigans* (recorded as *Pheidole moerens*) on in-coming goods (Wetterer and Wetterer 2004). Wetterer and Wetterer (2004) reported a male dacetine ant (Tribe Dacetini) that could not be identified to species level. It seems likely that this dacetine was one of the two newly reported *Strumigenys* species.

In their 2002 survey, Wetterer and Wetterer (2004) found *L. humile* in large numbers at all ten sites studied by Haskins and Haskins (1988). At four of the sites, they also found *P. megacephala* (Table 2). In 2016, I again found *L. humile* at all ten long-term survey sites, but found *P. megacephala* at only two (Table 2). At Spittal Pond, I found *L. humile* at the park entrance and parking lot where *P. megacephala* occurred in 2002. At Harrington 100s, I found *L. humile* north of Knapton Hill Road as before. South of Knapton Hill Road, rather than *P. megacephala*, I found high numbers of *P. navigans* and *T. simillimum*.

At two long-term survey sites, I found both *L. humile* and *P. megacephala*: on Ireland Island and the Newstead Hotel (now Newstead Belmont Hills Golf Resort and Spa). On Ireland Island, I found *P. megacephala* along the North Breakwater and by the Maritime Museum (now the National Museum) as before. In addition, I collected *P. megacephala* in front of the Clocktower Mall and to the south end of the Glassworks Mall, two places occupied by *L. humile* 14 years earlier, indicating a modest expansion of the *P. megacephala* population on North Ireland Island. At the Newstead Hotel, I found the boundary between *L. humile* and *P. megacephala* territory, near the western edge of the property, essentially identical as 14 years earlier. At the Newstead Hotel, I collected in the same vial *L. humile* and *P. megacephala* workers from only a few meters apart; the ants immediately locked in battle, confirming their mutual intolerance.

I found five ant species nesting in red mangrove in Bermuda: *L. humile* plus four Old World exotics that Wetterer and Wetterer (2004) did not collect in 2002: *Cardiocondyla minutior*, *Cardiocondyla obscurior*, *Monomorium floricola*, and *Plagiolepis alluaudi* (Table 3). At nine of the 14 sites, I found ants nesting inside twigs and branches: Hungary Bay (four samples with *M. floricola*, six with *P. alluaudi*), Crow Lane Park (one with *C. obscurior,* three with *M. floricola*), Trott's Pond (all ten with *P. alluaudi*), Walsingham Bay (four with *M. floricola,* one with *C. minutior*), Stokes Point Park (two with *L. humile*), Blue Hole (one with *M. floricola*), Mill Creek (two with *L. humile*), The Lagoon (one with *L. humile*), and Pilchard Bay (one with *C. obscurior,* two with *L. humile*). *Cardiocondyla obscurior* and *Monomorium floricola* are both almost exclusively arboreal species (Seifert 2003, Wetterer 2010).

At many red mangrove sites, I saw streams of *L. humile* on the branches of red mangrove growing in shallow water. In some cases, *L. humile* workers I found inside twigs could have belonged to land-based colonies, where they could access the man-

Table 1. Ants of Bermuda, arranged in descending order of the number of collection sites in 2002 (Wetterer and Wetterer 2004) plus the number of collection sites in 2016. + = recorded for the first time in 2016. NX = New World exotic. OX = Old World exotic.

Species	2002	2016	Dates	Status
Linepithema humile	27	38	1948–2016	NX
Pheidole megacephala	17	17	1889–2016	OX
Brachymyrmex cf. *obscurior*	19	9	1905–2016	native?
Brachymyrmex cf. *heeri*	6	8	1905–2016	native?
Solenopsis sp. thief ant	4	8	1934–2016	native?
Paratrechina longicornis	7	4	1990–2016	OX
Hypoponera opaciceps	4	4	1905–2016	native?
+*Pheidole navigans*		6	2016	NX
Tetramorium simillimum	2	4	1922–2016	OX
Tetramorium caldarium	1	4	2002–2016	OX
Monomorium floricola		4	2009–2016	OX
Odontomachus ruginodis	1	2	1889–2016	native?
+*Strumigenys membranifera*		3	2016	OX
Camponotus pennsylvanicus	2		2001–2002	NX
Cardiocondyla emeryi	1	1	1905–2002	OX
Cardiocondyla obscurior	2		1987–2016	OX
Monomorium monomorium	1	1	1900–2016	OX
Plagiolepis alluaudi		2	1945–2016	OX
+*Cardiocondyla minutior*	1		2016	OX
+*Strumigenys emmae*	1		2016	OX
Crematogaster sp. male			1987	native?
Wasmannia auropunctata			1925–1966	NX
Nylanderia vividula			1905–1925	OX
Hypoponera punctatissima			1910	OX
Nylanderia cf. *fulva*			1905	NX

Table 2. Ten sites surveyed repeatedly by Haskins and Haskins (1988), Wetterer and Wetterer (2004), and the present study in 2016. P = *Pheidole megacephala*, L = *Linepithema humile*, both = both species, - = not surveyed. (See Methods for more detailed site information.)

Site	Year					
	1963	1966	1973	1986	2002	2016
Great Head Park	–	–	both	L	L	L
Mullet Bay Rd. & Ferry Road	P	both	both	L	L	L
Leamington Caves	L	–	P	L	L	L
Knapton Hill Rd Intersection	L	–	both	L	L	L
Knapton Hill Rd & Harrington 100s	L	–	P	L	both	L
Christchurch & Brighton Hill	both	–	P	L	L	L
Spittal Pond	P	–	P	P	both	L
Newstead Hotel	L	–	L	both	both	both
Wreck Road	both	–	P	P	L	L
Ireland Island	–	P	–	P	both	both
% observations = *P. megacephala*	40	67	67	36	29	17

Table 3. Ants nesting in dead twig and branch samples from red mangrove, arranged in descending order of number of collection sites.

	# sites	# samples
Monomorium floricola	4	12
Linepithema humile	4	7
Plagiolepis alluaudi	2	16
Cardiocondyla obscurior	2	2
Cardiocondyla minutior	1	1

grove growing in water via a continuous canopy. However, one sample from Pilchard Bay that had *L. humile* inside twigs came from a small mangrove island consisting of two mangrove trees isolated by water from all other mangroves. This *L. humile* colony had to be completely arboreal.

All three samples that people sent me from their houses included *L. humile*. One also included *P. megacephala* and *Brachymyrmex* cf. *heeri*, and one included *P. navigans*.

Discussion

In 2016, I found that *L. humile* dominated most sites I surveyed in Bermuda. Still, *P. megacephala* occupied substantial areas, particularly in and around the capital of Hamilton. *Pheidole megacephala* is a dominant species in tropical sites around the world, whereas *Linepithema humile* tends to dominate in subtropical areas with "Mediterranean" climates. It appears that *L. humile* may be better suited to the subtropical climate of Bermuda, except perhaps in warmer and sunnier habitats, such as the plantings along urban streets and in open parks, where *P. megacephala* may have the advantage.

One ant species that is possibly native to Bermuda is the trap-jaw ant *Odontomachus ruginodis*. This species was once common in Bermuda, but now appears to be quite rare (Haskins and Haskins 1965). *Odontomachus ruginodis* is common in South Florida and the West Indies. Although it is not known as a tramp species, Deyrup (1992) considered it to be probably exotic to Florida. Genetic analyses could help determine whether *Odontomachus ruginodis* (or any other ant species) is native or exotic to Bermuda.

Bermuda has the northernmost populations of mangroves in the world (Spalding et al. 2010). I surveyed ants in the red mangroves of Bermuda in the hope of finding some rare ants that use this unique habitat as a refuge and thus escaped extermination by *P. megacephala* and *L. humile*. However, because *L. humile* also nests in red mangrove, this habitat did not provide a refuge for ant species incapable of co-existing with this dominant species. Except for *L. humile*, all ant species I found nesting in the red mangroves of Bermuda were Old World exotics. Thus, red mangroves may serve as a refuge from the dominant invasive ants, but the only ants taking advantage of this refuge are other exotic species.

In the absence of invader-free refuges, invasive ants can drive native species to extinction. For example, in 2003, I surveyed ants on Monte Gordo, the highest mountain of the Atlantic island of São Nicolau, Cape Verde, and found only *P. megacephala* at all sites sampled except for sites within 100 m of the mountain's peak (JKW, unpublished data). Here, where *P. megacephala* had not yet spread, a small pocket of other ant species survived, including an endemic species known only from this mountain, *Monomorium boltoni*. If *P. megacephala* continues its spread up the mountain, it seems unlikely that *M. boltoni* will survive once *P. megacephala* overruns what may be its last refuge. Similarly, it may be that all ant species originally native to Bermuda are now extinct.

I was surprised to collect *P. navigans* at five sites scattered across Bermuda (and I was sent specimens from a sixth site), given that this species had never before been collected in Bermuda, and that I surveyed three of these same locales in 2002. This suggests that *P. navigans* may be a recent arrival on Bermuda and is spreading quickly. Curiously, at four of the five sites, *P. navigans* was coexisting with *L. humile*. On Ordnance Island, I even found them nesting together under the same piece of concrete. It would be interesting to determine whether or not *P. megacephala* can tolerate *P. navigans*. *Pheidole navigans*, a big-headed ant native to the Neotropics, is known as an exotic in the southeastern US (formerly misidentified as *P. moerens*; see Sarnat et al. 2015). If *P. navigans* battles with *P. megacephala*, but not with *L. humile*, the presence of *P. navigans* could affect the competitive balance between *P. megacephala* and *L. humile*.

Pheidole megacephala and *L. humile* began their worldwide dispersal in the 19th century and have already spread through much of their potential range (Wetterer et al. 2009; Wetterer 2012). However, several other highly destructive ants have thus far come to occupy only a small portion of their potential ranges, most notably the red imported fire ant (*Solenopsis invicta*) (Wetterer 2013). Great vigilance is needed to prevent *S. invicta* and other invasive ant species from reaching Bermuda where it would likely thrive (Morrison et al. 2004) and cause substantial ecological and economic damage.

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Supplementary material 1

Specimen collection information

Authors: James K. Wetterer

Data type: specimens data

Explanation note: Self-explanatory